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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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Vol. 50 No. 12

BULLETIN
OF THE
TORREY BOTANICAL CLUB

DECEMBER, 1923

Studies in the genus Lupinus—IX. Lupinus bicolor

CHARLES PIPER SMITH

(WITH SEVEN TEXT FIGURES)

This species, like *L. nanus*, the subject of my last paper (Bull. Torrey Club **50**: 159. 1923), is so abundant, variable, and widely distributed that its consideration absorbs all the space available at this time. The next paper, however, will complete my treatment of the *Micranthi*, including a key to the species recognized. Of these the following is the sixth species in the linear arrangement adopted.

6a. LUPINUS BICOLOR Lindl. Bot. Reg. **13**: *pl. 1109*. 1827. [FIG. 85.]

Lupinus micranthus bicolor Wats. Proc. Am. Acad. **8**: 536. 1873.

Lupinus sabulosus Heller, Muhlenbergia **7**: 9. 1911.

Lupinus strigulosus Gandoger, Bull. Soc. Bot. France **60**: 461. 1913.

Annual, fibrous, erect and simple, or diffusely branched at the base, 8–40 cm. tall, usually villous; leaves few or many, pubescent on both sides; petioles 3–7 cm. long; stipules subulate, 5–10 mm. long; leaflets five to seven, oblanceolate or cuneate, acute or obtuse, 10–20 mm. long by 2–5 mm. wide; peduncles 3–7 cm. long, racemes 1–7 cm. long, verticils one to three; flowers 8–12 mm. whorled, scattered, or umbellate by reduction of the raceme; bracts subulate, deciduous, pedicels slender, 1–3 mm. long; calyx minutely bracteolate or ebracteolate, upper-lip bifid, 2–4 mm. long, lower-lip minutely three-toothed or entire, 4–6 mm. long; petals blue and white, banner about 8 mm. long by 6–8 mm. wide, obovate, elliptic, rhombic, to orbicular-obovate, angled to emarginate, the purple-dotted white center changing to violet, the sides much reflexed, wings oblong to elliptical, 6–8 by 4–5 mm., keel slender, acute, arcuate or nearly

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straight, the slender acumen well defined, ciliate above between middle and apex; pods 15–20 mm. long by 3–5 mm. wide, appressed-hairy, ovules five to eight; seeds rhombic or elliptic-oblong, 2–3 mm. long by about 1.5 mm. wide, pale flesh-color, pearly-white, or grayish, unmarked or dotted or mottled with gray or brown, with or without an oblique lateral line.

Heller's recent review of this species (Muhlenbergia **7**: 6. 1911) permits me to omit here quotations from the original description and detailed references to the older literature.

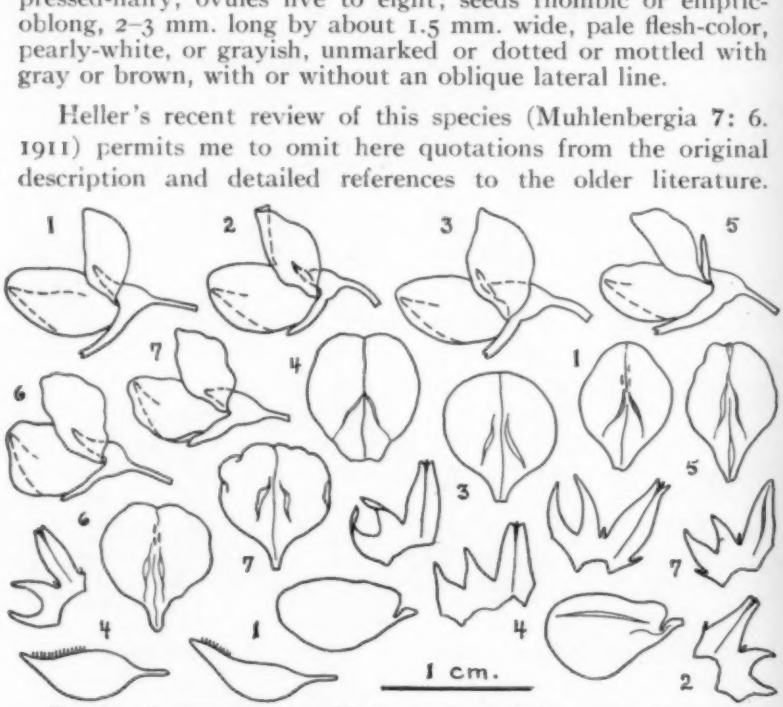

FIG. 85. LUPINUS BICOLOR Lindl. 1. *A. A. Heller 10069*, Vancouver, Wn. (CPS); 2. *J. Macoun 78892*, Vancouver Island (B); 3. *F. X. Williams*, San Francisco (CPS); 4. *C. F. Baker 816*, San Mateo County (UC); 5. *A. Eastwood 1*, Santa Barbara County (CPS); 6. *A. A. Heller 11227*, Butte County (CA); 7. *W. N. Suksdorf 5928*, Bingen, Wn. (CPS).

I can easily accept his conception, as to the typical form of the species, but I cannot follow his idea as to its limitations. Since my former published reference to this species (Muhlenbergia **6**: 137. 1911), I have had much more experience with it both in the field and the herbarium, and now see it as another of those species which consist of a large number of mutating or intergrading forms which almost defy classification. As in *L. sparsiflorus*, *L. concinnus*, and *L. nanus*, the wide variation in the shape of the leaflets in *L. bicolor* has much tempted me to recognize several varieties additional to those distinguished below; but here, especially, the inconstancies evident have led me to trim the list to just seven forms.

I have much desired to allow *L. sabulosus* varietal rank, but the differentiating characters well shown by Heller's drawings do not check up geographically. According to his drawings, his *10244*, from San Francisco, distributed as *L. sabulosus*, must be called *L. bicolor*, while several specimens from northern California and Vancouver Island should be referred to *L. sabulosus*. In truth, variation in the shape of the banner and in the size and color of the seeds, as well as in the size and shape of the leaflets, is rife in this species. Also the blue pigment is often missing from the petals, giving pink or white flowers.

L. strigulosus Gandoger is another extreme that, in itself, is perhaps possible of differentiation; but intermediates are numerous and make their classification a hair-splitting process.

Specimens assigned to the species, *sensu stricto*, are:—

BRITISH COLUMBIA. Vancouver Island: Colwood, July, 1922, *C. F. Newcombe & C. P. Smith 3675* (CPS); Esquimalt, May, 1908, *J. Macoun 78891* (B); same, May, 1914, *J. K. Henry* (CA); Oak Bay, May, 1908, *J. Macoun 78889, 78892*, and *78893* (B); Victoria, May, 1901, *A. J. Pineo* (BP, UC); same, May, 1914 and 1915, *J. K. Henry* (CA); same, Beacon Hill, May, 1908, *J. Macoun 78890* (B); same, May, 1911, *C. F. Newcombe* (CPS); same, Clover Point, May, 1915, *C. F. Newcombe* (CPS); same, Oak Park, June, 1920, *A. Eastwood 9742* (CA); same, Thetis Lake, June, 1919, *C. F. Newcombe* (CPS).

WASHINGTON. Clarke County: Vancouver, May, 1910, *A. A. Heller 10069* (B, DS, UC, CPS). Island County: Whidbey Island, *N. L. Gardner* (UC). Klickitat County: Bingen, April and May, 1907, *W. N. Suksdorf 5928* (CPS); same, April and June, 1911, *W. N. Suksdorf 7204* (B, UC, CPS). Pierce County: Tacoma prairies, May, 1908, *J. B. Flett* (UC). San Juan County: Argyle hills, July, 1919, *Lucile Roush* (DS); Argyle, June and Aug., 1917, *S. M. & E. B. Zeller 923* (B).

OREGON. Coos County: Marshfield, July, 1911, *W. Hayden* (CA); same, June, 1914, *W. Hayden* (CPS). Marion County: Salem, May, 1911, *M. E. Peck 2265* (CPS); same, July, 1922, *C. P. Smith 3578* and *3585* (CPS). Wasco County: The Dalles, May, 1882, *T. Howell* (DS); same, April, 1902, *E. P. Sheldon 9154* (DS); same, May, 1906, *J. Lunell* (DS).

CALIFORNIA. Alameda County: Oakland hills, May, 1888, *E. L. Greene* (DS); same, Sky Line Boulevard, May, 1922, *C.*

P. Smith 3535 (CPS). Amador County: New York Falls, April, 1893, *G. Hansen 15* (DS); same, June, 1893, *G. Hansen 954* (DS). Butte County: Centerville, April, 1915, *A. A. Heller 11857* (B, CA, DS, UCX); Big Chico canyon, March, 1914, *A. A. Heller 11227* (CA, UCX); Chico, April, 1903, *E. B. Copeland*, Baker distribution 3032 (BP); Mud Creek canyon, April, 1919, *A. A. Heller 13109* (CA, UCX); Rock Creek hills, April, 1915, *A. A. Heller 11817* (CA, DS, UCX, US). Contra Costa County: near Moraga Valley, May, 1888, *E. L. Greene* (UC). Glenn County: Stony Creek, Orland, May, 1915, *A. A. Heller 11887* (DS, UCX). Humboldt County; Bucksport, June, 1900, *J. P. Tracy 838* (UC); same, May, 1911, *J. P. Tracy 3195* (DS); Hoopa Indian Reservation, June, 1901, *H. P. Chandler 1314* (UC). Marin County; Mill Valley, May, 1913, *K. Brandegee* (UC); Mount Tamalpais, April, 1922, *L. R. Abrams 8069* (DS, CPS); near Tennessee Bay, May, 1896, *A. Eastwood* (UC). Mendocino County: Fort Bragg, July, 1920, *C. D. Duncan 212* (DS); Ukiah, June, 1913, *A. Eastwood* (CA). Placer County: Newcastle, May, 1884, *M. K. Curran* (CA). Sacramento County: Folsom, April, 1883, *T. S. Brandegee* (CA). San Francisco County: Childrens' Hospital, April, 1911, *A. A. Heller 10244* (B, BP, DS, UCX, CPS); Forest Hill, April, 1914, *P. B. Kennedy 4644* (UCX); Marine Hospital, April, 1903, *A. A. Heller 6627* (B, BP, DS, UC); sand hills, May, 1903, *C. F. Baker 2837* (B, BP, UC); also some sixteen other collections. San Luis Obispo County: San Simeon, June, 1888, *M. K. Curran* (CA). San Mateo County: Coast Range summit, May, 1902, *C. F. Baker 816* (B, BP, CA, US); Montara Mountains, above Lake Pilarcitos, June, 1922, *C. P. Smith 3557* (CPS); San Bruno hills, April, 1903, *C. F. Baker 1888* (BP, CA, UC); also seven other collections. Santa Barbara County: Ellwood, May, 1908, *A. Eastwood 1* (CA, CPS); Rincon ranch, May, 1908, *A. Eastwood* (CA, CPS). Siskiyou County: Yreka, April, 1910, *G. D. Butler 1190* and *1252* (DS). Stanislaus County: Oakdale, April, 1922, *C. P. Smith 3476* (CPS). Sutter County: Sutter City, March, 1905, *A. A. Heller 7568* (B, DS, UC). Tuolumne County: near French Flat, April, 1919, *R. S. Ferris 1535* (CA, DS). Yolo County: Knights Landing, April, 1892, *F. P. Nutting* (UC).

Key to the varieties of Lupinus bicolor *

Keel non-ciliate, or with one to four stray cilia; flowers 5–8 mm. long.	*6d.* var. *Pipersmithii.*
Keel distinctly ciliate on upper edges, between middle and apex.	
Lower calyx-lip trifid; flowers 5–8 mm. long.	*6g.* var. *trifidus.*
Lower calyx-lip tridentate or subentire.	
Flowers 8–12 mm. long.	*6a. L. bicolor.*
Flowers 4–8 mm. long.	
Flowers 6–8 mm. long.	
Racemes reduced to one verticil, or with more or less of two.	*6b.* var. *umbellatus.*
Racemes of three to six, or more, verticils.	*6c.* var. *tridentatus.*
Flowers 4–6 mm. long.	
Pods five- to eight-seeded.	*6e.* var. *microphyllus.*
Pods four- or five-seeded.	*6f.* var. *tetraspermus.*

6b. **Lupinus bicolor umbellatus** (Greene) comb. nov. [FIG. 86.]

Lupinus umbellatus Greene, Bull. Cal. Acad. **2:** 145. 1886.

Differing only in the reduction in the racemes and flowers, the former usually reduced to one verticil, the latter in size to about 7 mm. long. Most, if not all, of the mainland collections referred here by the collectors I have considered it better to refer to other varieties of the species.

FIG. 86. LUPINUS BICOLOR UMBELLATUS (Greene) C. P. Smith. *T. S. Brandegee*, Santa Cruz Island (UC).

CALIFORNIA. Santa Barbara County: Santa Cruz Island, July and Aug., 1886, *E. L. Greene* (UC); same, April, 1888, *T. S. Brandegee* (UC); same, May, 1908, *Frida Niedermüller* (UC); same, 1919, *Mrs. A. Swain* (CA).

6c. **Lupinus bicolor tridentatus** Eastwood, var. nov. [FIG. 87.]

A planta typica differt floribus minoribus 6–8 mm. longis, labio inferiore calycis tridentato, vexillo elliptico ad obovato vel late spatulato, carina ciliata.

Differing from typical *L. bicolor* in the reduced size of the flowers, which are from 6–8 mm. long, in from three to six or more distinct verticils, the lower calyx-lip distinctly three-toothed. Greatly varying in stature, more commonly 15–25 cm. tall, but sometimes lower and again as much as 40 cm. tall.

* In following this key, use the minimum measurements for dried flowers only and the maximum measurements for fresh flowers only.

Abundant in the Coast Ranges of western Middle California, and apparently local, at scattered stations, elsewhere.

BRITISH COLUMBIA. Vancouver Island: Colwood, July, 1922, *F. C. Newcombe & C. P. Smith 3674* and *3676* (CPS).

WASHINGTON. Clarke County: Vancouver Lake, July, 1922, *C. P. Smith 3589* (CPS).

OREGON. Jackson County: Central Point, July, 1918, *A. A. Heller 13077* (DS, UCX). Linn County: Albany, May, 1922, *M. W. Gorman 5729* (CPS).

CALIFORNIA. Alameda County: Alameda, May, 1891, *E. L. Greene* (DS 36730); Oakland, March, 1864, *W. H. Brewer*

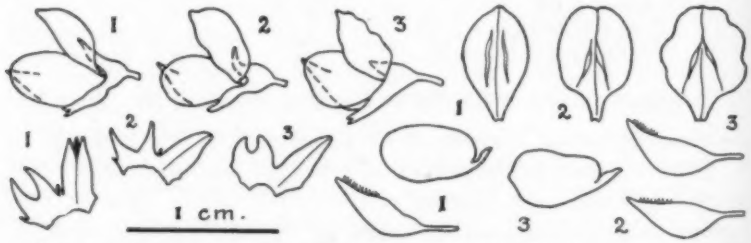

FIG. 87. LUPINUS BICOLOR TRIDENTATUS A. Eastwood. 1. *C. P. Smith 1422a*, San Mateo County (CPS); 2. *A. A. Heller 7836*, Kern County (UC); 3. *A. A. Heller 13077*, Oregon (CA).

2773 (CA, UC); between Mission San Jose and Livermore, April, 1904, *A. A. Heller 7314* (B, DS, UC, UCX); Sunol Valley, June, 1916, *L. R. Abrams 5698* (DS, CPS). Amador County: no locality, 1891, *G. Hansen* (UC); Ione, March, 1921, *A. Eastwood 10089* (CA). Contra Costa County: Antioch, April, 1922, *C. P. Smith 3492* (CPS); Mount Diablo, May, 1862, *W. H. Brewer 1149* (UC); Point Richmond, March, 1900, *J. P. Tracy 624* (UC). Eldorado County: Clarksville to Shingle Springs, April, 1911, *A. A. Heller 12285* (CA, DS, UCX). Humboldt County: Humboldt Bay, May, 1901, *H. P. Chandler 1146* (DS, UC); Trinidad Head, 1889, *W. R. Dudley* (DS); Van Duzan Valley, June–July, 1908, *J. P. Tracy 2693* (UC); Willow Creek, June, 1910, *L. R. Abrams 7172* (DS). Kern County: Tehachapi, May, 1905, *A. A. Heller 7836* (B, DS); same, *K. Brandegee* (CA, UC). Los Angeles County: Antelope, May, 1895, *A. Davidson* (UC); Antelope Valley foothills, May, 1902, *H. M. Hall 3053* (UC); near Los Angeles, June, 1904, *pupils of Los Angeles High School* (UC); Sierra Madre, June, 1914, *C. P. Smith 2880* (CPS).

Marin County: Mount Tamalpais, April, 1899, *A. Eastwood* (CA); Point Reyes Station, May, 1921, *C. P. Smith 3378* and *3379* (CPS); Ross Valley, April, 1892, *F. T. Bioletti* (UC). Mariposa County: Cathey Valley, April, 1915, *A. Eastwood 4351* (CA); Yosemite Valley, June, 1906, *Anna Head* (CA); same, June, 1911, *H. M. Hall 8871* (UC). Mendocino County: Russian River, Ukiah Valley, April, 1918, *L. R. Abrams 6976* and *6977* (DS, CPS); Wolf Creek, July, 1916, *L. R. Abrams 5862* (DS). Monterey County: Los Pesares, Santa Lucia Mountains, May, 1920, *L. R. Abrams 7354* (DS); Santa Lucia Mountains, June, 1901, *W. R. Dudley* (DS). Napa County: Calistoga, April, 1903, *C. F. Baker 1982* (BP). Orange County: Orange, April, 1902, *J. B. Davy* (UC). Placer County: Roseville, April, 1883, *T. S. Brandegee* (CA). Sacramento County: Fair Oaks, March, 1900, *M. S. Baker* (UC); Folsom, April, 1916, *A. A. Heller 12307* (CA, UCX). San Benito County: San Juan hill, May, 1922, *C. P. Smith 3514* (CPS). San Diego County: Cuyamaca Lake, June, 1903, *L. R. Abrams 3841* (DS); Descanso, May, 1906, *T. S. Brandegee* (B, UC); Ramona, April, 1903, *H. M. Hall 3866* (UC); Warners Springs, 1911, *Mrs. A. L. Coombs* (CA); Witch Creek, *R. D. Alderson*, plant III (UC). San Francisco County: Lake Merced, April, 1893, *W. R. Dudley* (DS). San Luis Obispo County: Arroyo Grande, May, 1895, *M. Alice King* (UC); Avila, *Mrs. R. W. Summers* (UC 55703, plant II). San Mateo County: near Colma, April, 1908, *C. P. Smith 1422a* (DS, CPS); Cooleys Landing, April, 1922, *E. A. McGregor* (CPS); Crystal Springs Lake, April, 1904, *L. R. Abrams* (DS, CPS); Lake San Andreas, April, 1903, *C. F. Baker 1921* (BP, UC). Santa Barbara County: Santa Barbara, May, 1918, *J. C. Carlson* (CA). Santa Clara County: Betabel, April, 1921, *C. P. Smith 3267* and *3268* (CPS); Black Mountain, May, 1903, *A. D. E. Elmer 4797* (BP, CA, DS, UC); Evergreen foothills, *J. B. Davy 95 A* (UC); Loma Prieta, April, 1894, *J. B. Davy 527*, *531*, and *635* (UC); Palo Alto, May, 1893 *I. Tidestrom* (UC); San Martin, March, 1901, *H. P. Chandler 909* (BP); Smith Creek Hotel, June, 1908, *C. P. Smith 1464* (DS, CPS); Wright, April, 1921, *C. P. Smith 3313* and *3314* (CPS); also about twenty-five other collections. Santa Cruz County: Capitola, April, 1903, *C. F. Baker 1963* (B, BP, UC); Glenwood, Sept., 1907, *H. Davis* (CPS); Santa Cruz, April, 1903, *A. A. Heller 6554* (B, BP, DS, UC, UCX)

Tuxedo, April, 1904, *W. R. Dudley* (DS). Shasta County: Anderson, April, 1918, *A. A. Heller 12991* (CA); Redding, 7 miles south, April, 1917, *A. A. Heller 12992* (CA). Sonoma County: Santa Rosa, April, 1921, *A. Eastwood 10369* (CA, TYPE). Sutter County: Marysville Buttes, May, 1914, *A. A. Heller* (DS); same, April, 1914, *A. A. Heller 11255* (CA, UCX); same, March, 1905, *A. A. Heller 7574* (B, UC, CPS). Tuolumne County: Bear Creek, April, 1896, *C. A. Purpus 1726* (UC); Grape Vine Spring, March, 1898, *P. S. Woolsey* (UC, 126973, II); Kaweah, April, 1903, *R. Hopping 550* (UC).

6d. **Lupinus bicolor Pipersmithii** (Heller) comb. nov. [FIG. 88.]

Lupinus Pipersmithii Heller, Muhlenbergia **7:** 93. *f. 16–17.* 1911.

Differing from typical *L. bicolor* in reduction of size of flowers which are from 5–8 mm. long, and in the non-ciliate keel. The seeds are usually pale flesh-colored, more or less mottled with yellowish-brown.

When I first found this interesting variation, I really considered it to be a worthy species (Muhlenbergia **6:** 139–141. 1911), in comparison with its relatives then known to me; but now, after much more extensive experience with it and *L. bicolor*, I must classify it where my judgment says it belongs. Except for the lack of keel-ciliation, it can not be distinguished from var. *tridentatus* at Antioch, Betabel, and San Juan, nor from var. *microphyllus* at many points in the San Joaquin Valley. It is the dominant form of *L. bicolor* in the last locality and seems to be local and less common elsewhere. Since Heller's description is readily available it is not reproduced here.

CALIFORNIA. Amador County: Ione, March, 1921, *A. Eastwood 10079* (CA). Contra Costa County: Antioch, April, 1889, *Chestnut & Drew* (UC); same, April, 1903, *C. F. Baker 2822* (BP, CA, UC); same, April, 1921, *A. Eastwood 10280* and *10306* (CA); same, April, 1922, *C. P. Smith 3482* (CPS); Brentwood, May, 1893, *A. Eastwood* (CA); Byron Springs, March, 1914, *A. Eastwood 3784* (CA). Fresno County: Big Sandy Creek, April, 1915, *Julia McDonald* (CA); Clovis, April, 1902, *C. H. Thompson* (DS, CPS); Pollasky, April, 1906, *A. A. Heller 8154* (B, CA, DS). Glenn County: Orland, Stony Creek, May, 1915, *A. A. Heller 11886* (CA, DS, UCX). Madera

County; Madera, April–May, 1896, *J. B. Davy 1698* (UC); same, April, 1897, *W. A. Setchell* (UC). Mariposa County: Blochman ranch, April, 1915, *A. Eastwood 4253* (CA). Merced County: Merced, April, 1915, *A. Eastwood 4423* (CA); Livingston, April, 1922, *Edith M. Smith & J. C. Menker 120* (CPS). Monterey County: Mansfield ranch, Santa Lucia Mountains, May, 1897, *A. Eastwood* (CA); same, April, 1915, *A. Eastwood 4072* (CA); San Lucas, March, 1922, *Edith M. Smith 108* (CPS). Napa County: Palisade, New Pope Valley, May, 1893, *W. L. Jepson* (UC). Riverside County: Banning, 1904, *M. F. Gilman* (UC); Banta, April, 1897, *A. Eastwood* (CA). Sacramento County: Del Paso Park, April, 1920, *A. A. Heller 13384* (UCX).

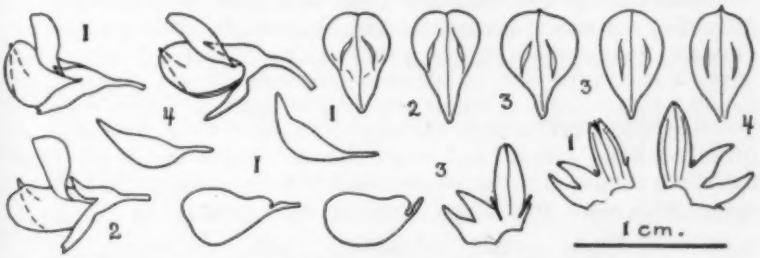

FIG. 88. LUPINUS BICOLOR PIPERSMITHII (Heller) C. P. Smith. 1. *C. P. Smith 1403* (CPS); 2. *C. P. Smith 1402* (CPS); 3. *C. P. Smith 3264* (CPS); 4. *C. P. Smith 3266* (CPS).

San Benito County: San Juan, May, 1903, *A. D. E. Elmer 4914* (CA, DS); same, May, 1922, *C. P. Smith 3517* (CPS). San Francisco County: April, 1886, *T. S. Brandegee* (CA). San Joaquin County: Live Oaks, March, 1877, *V. Rattan* (DS); Stockton, April, 1922, *C. P. Smith 3471* (CPS); Tracy, 1892, *F. T. Bioletti* (UC); same, April, 1903, *C. F. Baker 2910* (BP, UC, US); same, April, 1922, *C. P. Smith 3471* (CPS); Waverly, 1890–91, *J. A. Sanford* (UC). San Luis Obispo County: Paso Robles, March, 1899, *J. H. Barber* (UC). San Mateo County: Stanford Park, April, 1911, *J. I. McMurphey* (DS, CPS); near Stanford University, April, 1908, *C. P. Smith 1402* and *1403* (B, DS, CPS); same, April, 1911, *A. A. Heller 10250* (B, UC, UCX, CPS); same, *A. A. Heller 10251* (UC). Santa Clara County: Betabel, April, 1921, *C. P. Smith 3264* and *3266* (CPS); Gilroy, April, 1921, *C. P. Smith 3257* (CPS); Stanford University, April, 1911, *A. A. Heller 10253* (B, BP, DS, CPS). Santa Cruz

County: Chittenden, April, 1921, *C. P. Smith 3260* (CPS); Glenwood, 1914, *H. Davis* (CA); Rays, June, 1890, *W. Price* (CA). Stanislaus County: Ceres, April, 1916, *W. W. Wagner* (DS); Modesto, 1917, *K. Brandegee* (UC); Oakdale, April, 1922, *C. P. Smith 3477* (CPS). Tulare County: Tulare, April, 1897, *J. B. Davy 3048* (UC); same, March, 1914. *A. Eastwood 384* (CA).

6e. **Lupinus bicolor microphyllus** (Wats.) comb. nov. [FIG. 89.]

Lupinus micranthus microphyllus Wats. Proc. Am. Acad. **8:** 535. 1873.

Lupinus rostratus Eastwood, Proc. Cal. Acad. II. **6:** 424. *pl. 56.* 1896.

Plants 10–40 cm. tall, the branches depressed, decumbent, ascending, or erect; leaflets linear-oblanceolate, oblanceolate, or cuneate, 6–25 mm. long, 1.5–3 mm. wide; flowers 4–5 mm. long, verticillate, umbellate, or alternate, banner elliptic, obovate, or orbicular-spatulate, acute or rounded at apex, 5–7 mm. long by 2–4 mm. wide, keel commonly nearly straight, though sometimes quite arcuate, ciliate and with slender, acute acumen; pods usually 10–15 mm. long; seeds usually pale in color, but sometimes with dark markings, about 2 mm. long.

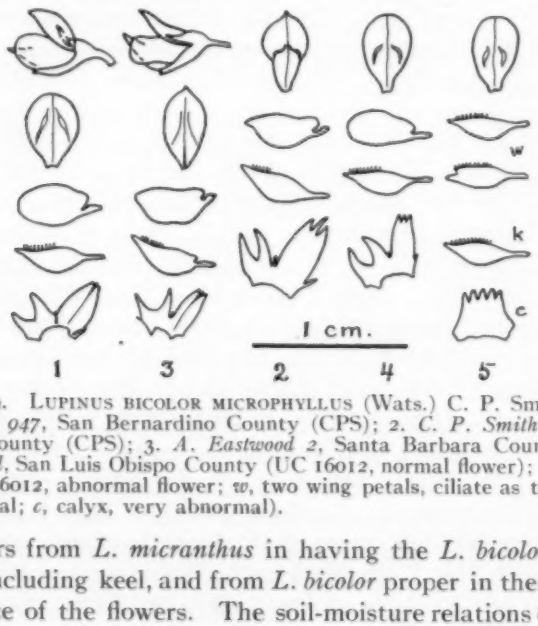

FIG. 89. LUPINUS BICOLOR MICROPHYLLUS (Wats.) C. P. Smith. 1. *G. L. Moxley 947*, San Bernardino County (CPS); 2. *C. P. Smith 2854*, Los Angeles County (CPS); 3. *A. Eastwood 2*, Santa Barbara County (CPS); 4. *L. Jared*, San Luis Obispo County (UC 16012, normal flower); 5. Same as last (UC 16012, abnormal flower; *w*, two wing petals, ciliate as the keel; *k*, keel, normal; *c*, calyx, very abnormal).

Differs from *L. micranthus* in having the *L. bicolor* type of flower, including keel, and from *L. bicolor* proper in the much reduced size of the flowers. The soil-moisture relations evidently

have much to do with the stature, size of leaflets, length and density of pubescence, and, perhaps, color of the seeds. Watson's characterization of the variety is not much in itself, but I am satisfied that the plants assigned here include the form for which Watson borrowed Nuttall's manuscript name. The original description is as follows:

(*L. microphyllus*, Nutt. MS.) A lower and more hirsute form, with leaflets 3–6 lines long. San Diego.

L. rostratus Eastwood is, as I see it, a teratological variation, in line with *L. scaposus* Rydb. (see Bull. Torrey Club **46:** 397. 1919).

This is the dominant variety in Southern California, where it has long been known as *L. micranthus*. From this region, where it is evidently very common, it extends locally northward as far as southern Oregon. I include here two of Greene's manuscript species.

OREGON. Yamhill County: dry open slopes, May, 1878, *Mrs. R. W. Summers 155* (UC).

CALIFORNIA. Amador County: Ione, *K. Brandegee* (CA); Jackson, May, 1891, *G. Hansen 339* (DS). Butte County: Chico, April, 1903, *E. P. Copeland*, Baker distribution 3032 (UC). Calaveras County: Mokelumne Hill, *F. E. Blaisdell* (CA, CPS). Contra Costa County: Brentwood, May, 1893, *A. Eastwood* (CA); Point Isabel, July, 1911, *K. Brandegee* (UC). Eldorado County: Pilot Hill, April, 1915, and May, 1909, *K. Brandegee* (UC). Fresno County: Zapato, March, 1893, *A. Eastwood* (CA); Big Sandy Creek, April, 1915, and April, 1916, *Julia McDonald* (CA). Glenn County: Colusa, April, 1921, *A. Eastwood 10244* (CA). Humboldt County: Willow Creek, May, 1919, *J. P. Tracy 5149* (UC). Kern County: Bakersfield, April, 1893, *A. Eastwood* (CA); Caliente, *K. Brandegee* (UC); same, April, *T. S. Brandegee* (CA); Delano, April, 1893, *A. Eastwood* (CA); Havilah, *K. Brandegee* (UC); Isabella, April, 1915, *B. W. Evermann* (CA); Kernville, May, *T. S. Brandegee* (CA). Lake County: Lower Lake, May, 1903, *C. F. Baker 2983* (BP, UC, US). Los Angeles County: Barley Flats, San Gabriel Mountains, July, 1921, *G. L. Moxley 1028* (CPS); Ballona hills, March, 1921, *G. L. Moxley 906* and *940* (CPS); Antelope Valley, south side, May, 1902, *H. M. Hall 3068* (UC); Los Angeles, Feb., 1902, and April, 1903, *Miss E. D. Palmer* (UC); Manzana, May,

1896, *J. B. Davy 2544* (UC); Pasadena, April, 1905, *G. B. Grant* (CA, DS, UC); Santa Catalina, May, 1916, *K. Brandegee* (UC); Santa Monica Mountains, March, 1916, *Crawford & Hiatt* (BP); plus some thirty other collections. Mariposa County: Blochman ranch, *A. Eastwood 4253* (CA). Monterey County: Big Pinnacles, April, 1919, *R. S. Ferris 1734* (DS); Jolon, April, 1915, *A. Eastwood 4142* (CA); Pacific Grove, March, 1921, *Edith M. Smith 103* (CPS); San Antonio Creek, May, 1895, *W. R. Dudley* (DS); Sur River, June, 1893, *A. Eastwood* (CA). Riverside County: Banning, March, 1919, *Munz, Street, & Williams 2375* (BP, DS); Cabazon, March, 1919, *Munz, Street, & Williams 2460* (BP); Corn Springs, Chuckwalla Mountains, April, 1922, *P. A. Munz & D. Keck 4845* (CPS); Hemet, April, 1904, *C. F. Baker 4100* (BP, DS); Keen Camp, May, 1922, *F. W. Pierson 3064* (CPS); same, *Munz & Johnston 5427* (CPS); Sedco Station, April, 1922, *P. A. Munz 5079* (CPS). San Benito County: Hernandez, April, 1903, *Laura M. Lathrop* (DS); Tres Pinos, March, 1893, *W. W. Price* (DS). San Bernardino County: Colton, April, 1882, *M. E. Jones 3330* (CA); Hesperia, April, 1888, *S. B. Parish* (UC); same, May, 1920, *I. M. Johnston* (BP); same, May, 1921, *G. L. Moxley 947* (CPS); San Bernardino, April, 1901, *S. B. Parish 4659* and *4662* (DS); Upland, Red Hill, April, 1918, *P. A. Munz 2103* and *2104* (BP); same, *I. M. Johnston 1871*, *1974* and *1975* (BP, DS); Yucaipe Valley, May, 1918, *S. B. Parish 11793* (BP); also a few others. San Diego County: Bonsal, May, 1920, *Munz & Harwood 3918* (CPS); Campo, Warren ranch, April, 1920, *A. Eastwood 9391*, *9392*, and *9472* (CA); Cuyamaca Lake, July, 1895, *S. G. Stokes* (DS); Descanso, June, 1919, *A. Eastwood 9177*, *9177a*, and *9178* (CA); Live Oak Springs, Laguna Mountains, June, 1917, *E. A. McGregor 925* (DS); San Diego, April, 1903, *T. S. Brandegee*, Baker distribution 3363 (B, BP, CA, DS, UC); Witch Creek, 1919, *R. D. Alderson* (UC, plants I and II); also some fifteen others. San Francisco County: April, *K. Curran* (CA). San Luis Obispo County: Avila, *Mrs. R. W. Summers* (UC); Estrella, *L. Jared* (CA, DS, UC); Paso Robles, May, 1920, *A. J. Perkins* (CPS); Pismo, June, 1884, *Mrs. R. W. Summers* (UC); San Luis Obispo, 1886, *M. M. Miles* (CA); Santa Margarita Mountain, April, 1903, *W. R. Dudley* (DS). Santa Barbara County: Ellwood, May, 1908, *A. Eastwood 2* (CA, CPS); Santa Barbara,

1888, *T. S. Brandegee* (CA); Santa Maria, June, 1906, *A. Eastwood 359* (CA); Surf, Antonio siding, *K. Brandegee* (UC). Santa Clara County: Los Gatos, April, 1897, *W. A. Setchell* (UC); San Martin, March, 1915, *L. R. Abrams 5179* (DS); Stanford University foothills, May, 1902, *C. F. Baker 845* (BP, CA, UC); Uvas road, May, 1922, *C. P. Smith 3510* (CPS). Santa Cruz County: Olympia, June, 1921, *C. P. Smith 3403* (CPS). Shasta County: Anderson, April, 1918, *A. A. Heller 12991* (UCX). Sonoma County: Healdsburg, April, 1897, *M. Alice King* (BP, UC). Stanislaus County: March, 1921, *Mrs. B. Hoisholt 104* (CPS); same, *Estella Hoisholt 101* (CPS); same, April, 1922, *C. P. Smith 3473* (CPS). Sutter County: Marysville Buttes, April, 1917, *R. S. Ferris 649* (DS). Tulare County: between Earlimart and Delano, May, 1914, *A. Eastwood 3959* (CA); Grapevine Springs, March, 1898, *P. S. Woolsey* (UC, plant I); Milo, April, 1900, *W. R. Dudley* (DS); Porterville, April, 1907, *Miss L. L. Donnelly 32* (UC); Tule River, March, 1897, *W. R. Dudley* (DS). Ventura County: Mutau Flat, June, 1908, *Abrams & McGregor 190* (DS); Nordhoff, April, 1916, *A. Eastwood* (CA); Ojai, April, 1896, *F. W. Hubby 36* and *37* (UC); Santa Paula, April, 1902, *J. B. Davy* (UC); Ventura, Foster Park, April, 1916, *A. Eastwood 5006* (CA).

LOWER CALIFORNIA. Guadalupe Island, 1898, *Harry Drent* (UC); same, June, 1906, *Brown* (UC); San Sebastian, April, 1889, *T. S. Brandegee* (CA, UC).

SONORA. Casita, May, 1892, *T. S. Brandegee* (UC).

6f. **Lupinus bicolor tetraspermus** var. nov. [FIG. 90.]

Varietas caulibus petiolisque angustissimis; foliolis linearefiliformibus; floribus 4–5 mm. longis, labio superiore calycis 2 mm. longo inferiore 3 mm. longo, vexillo late obovato, carina ciliata; leguminibus 10–12 mm. longis, 3 mm. latis, aliquantum constrictis, seminibus saepius quattuor, interdum quinque permaculatis vix 2 mm. longis.

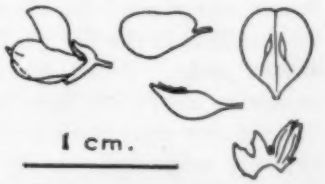

FIG. 90. LUPINUS BICOLOR TETRASPERMUS C. P. Smith. *C. P. Smith 3405* (CPS).

Stems and petioles filiform, leaflets linear-filiform, 10–20 mm. long; flowers 4–5 mm. long, banner orbicular-obovate, 6 mm. long by 5 mm. wide, keel ciliate, upper

calyx-lip 2 mm. long, lower 3 mm. long; pods 10–12 mm. long, 3 mm. wide, much constricted, suggesting those of *Vicia tetrasperma*; seeds more often four, but sometimes five, scarcely 2 mm. long by about 1.5 mm. wide, heavily marked.

CALIFORNIA. Santa Clara County: Wright, June, 1921, *C. P. Smith 3405* (TYPE, DS; type-duplicates CA, G, UC, CPS).

This is a very odd extreme with the aspect of a good species, but undoubtedly to be considered a variety of *L. bicolor*.

6g. **Lupinus bicolor trifidus** (Torr.) comb. nov. [FIG. 91.]

Lupinus micranthus trifidus Wats. Proc. Am. Acad. **8:** 535. 1873.
Lupinus trifidus Torr.; Wats. Proc. Am. Acad. **12:** 250. 1877.

Watson's second characterization of this form is as follows:

> Very closely resembling *L. micranthus*, but the lower lip deeply 3-cleft with linear segments: pod narrower and shorter (about 6 lines long and 1½ broad), usually 5–6-seeded: seeds a line broad, uniformly mottled: flowers 3 lines long or less, mostly in a single terminal whorl.—*L. micranthus*, var. *trifidus* Watson, Rev. Lup. 535. Near San Francisco, by various collectors, and recently in fine specimens by Mr. G. R. Vasey. The ordinary *L. micranthus*, besides the nearly entire lip, has a pod often an inch long and 2½ lines broad, 6–9-seeded, and the large seeds variously mottled, but with a lighter spot around the sometimes dark eye.

Although I once (Muhlenbergia **6:** 137. 1911) held this to be a distinct species, I now see no substantial excuse for so treating it. Its relationship, however, is evidently with *L. bicolor* rather than with *L. micranthus*. Its deeply trifid lower calyx-lip is its one outstanding peculiarity.

Seemingly peculiar to the San Francisco and Monterey sandy areas, its occurrence at San Juan, San Benito County, calls for special consideration. Elmer's specimens show a habit and stature not at all like the usual plants, and the calyx character (see figure) was not recognized by me until dissection of a flower was made. In May, 1922, I visited San Juan to study this variant in the field; but I found vars. *tridentatus* and *Pipersmithii* only. While Elmer's plants may represent a non-persisting mutation from the common var. *tridentatus*, I hold the opinion that they are mere non-persisting climatic or soil variants originating from seed casually introduced from the Monterey region, San Juan being on the much traveled San Francisco-Monterey highway.

CALIFORNIA. Monterey County: Del Monte, May, 1888, *B. F. Leeds* (DS); same, March, 1921, *C. P. Smith 3241* and

3244 (CPS); Pacific Grove, April, 1902, *A. D. E. Elmer 3512* (UC); same, April, 1903, *A. A. Heller 6631* (B, BP, DS, UC); June, 1907, *C. P. Smith 1358* (CPS); same, March, 1921, *Edith M. Smith 105*, *106*, and *107* (CPS); Seaside, April, 1894, *W. R. Dudley* (DS); same, March, 1910, *Alice D. Randall 230* (DS). San Benito County: San Juan, May, 1903, *A. D. E. Elmer 4910* (BP, DS). San Francisco County: Lake Merced, May, 1893, *Michener & Bioletti* (UC); San Francisco, May, 1884, *M. K. Curran* (DS, UC); same, Jan., 1893, *J. B. Davy 1169* (UC). San Mateo County: Colma, back of cemeteries, April, 1908, *C. P. Smith 1423* (DS, CPS); South San Francisco, April, 1908, *C. P. Smith 1419* (CPS).

Lupinus bicolor, as herein interpreted, would form a most interesting subject for genetic investigations, such as recently concluded and reported upon by Dr. Burlingame (Am. Nat. **55**: 427–448. 1921).

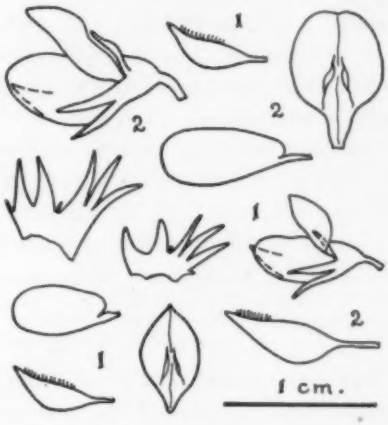

FIG. 91. LUPINUS BICOLOR TRIFIDUS (Torr.) C. P. Smith. 1. *C. P. Smith 1423*, San Francisco (CPS); 2. *A. D. E. Elmer 4910*, San Juan (DS).

The following list will identify the abbreviations here used in the citation of specimens examined:

B, Brooklyn Botanic Garden;

BP, C. F. Baker Herbarium, Pomona College, Claremont, California;

CA, California Academy of Science, San Francisco;

CPS, herbarium of the writer;

DS, Dudley Herbarium, Stanford University;

G, Gray Herbarium, Harvard University;

NY, New York Botanical Garden;

UC, Department of Botany, University of California;

UCX, Division of Agronony, University of California Experiment Station;

US, United States National Herbarium.

SAN JOSE, CALIFORNIA

Intracellular relations of aggregate crystals in the spadix of Anthurium

L. O. Gaiser

(WITH PLATE 20)

The current views as to the relation of crystals to other contents of the cell, and especially the nucleus, have recently been sharply questioned by Jeffrey (**5**). Jeffrey denies that the compound crystals of calcium oxalate, found abundantly by him in the pith, cortex, and phloem of *Ginkgo*, as well as in some of the Dicotyledons, arise by a process of crystallization in the fluid of the cell sap. He considers *Ginkgo* the most favorable for study and finds that cells near the growing point, which are to contain crystals, are easily distinguishable by a centrally placed nucleus about which the crystals are formed. He states:

> From the very beginning the crystals occupy practically the whole lumen of the cell and more or less protoplasm surrounds the nucleus which is the organic centre of the druses. The crystals in fact constitute an irregular spiny casing which surrounds the nucleus and protoplasm.

He states further that "in very large and old crystals indications of the presence of a nucleus can frequently be demonstrated by appropriate methods." Species of the dicotyledonous families Juglandaceae, Cactaceae, Begoniaceae, and Geraniaceae differ from *Ginkgo* in that "the nucleus becomes obscured at a much earlier stage of development of the crystal and not infrequently the latter does not occupy the whole lumen of the cell as in *Ginkgo*."

Lloyd (**9**), on the other hand, in a further study of leaves from growing buds of *Ginkgo*, confirms the commonly accepted view and finds in older cells, in which the crystals were large enough to occupy the greater portion of the total volume of the cell, the nucleus crowded against the cell wall and between projecting crystals of the druse. He speaks also of "colloidal material being imprisoned in the druse." Jeffrey (**6**), however, in a second paper nowhere speaks of the nucleus being surrounded by the crystal but makes such statements as the following: "The central body in crystals is in fact not only clearly observable but is likewise very far from being unsubstantial."

While making a more general cytological study of *Anthurium* I have observed numerous cells containing stellate crystals in which the relations of these crystals to the nucleus and other cell elements can be seen with great clearness. There is an abundant literature dealing with the position of the crystals in plant cells. Wakker (**23**), using De Vries' method, 10 per cent potassium nitrate and eosin solution, for studying the vacuolar membrane, examined cells of *Anthurium Hookeri*, containing various crystal formations. For such studies the crystal druses, he claims, give the greatest difficulty since the plasma and vacuole wall die simultaneously and it is thus difficult to isolate the vacuoles. However, occasionally favorable preparations were obtained and he describes a cell containing a vacuole in which lay a very young druse. He gives no illustrations of the *Anthurium* but for *Hoya carnosa* figures a cell from a leaf showing very clearly that the stellate crystal there lies in the vacuole. For *Ricinus communis* a row of cells gives similar evidence. After a detailed description of the finding of crystals in vacuoles in *Hoya carnosa*, *Anthurium Hookeri*, and *Ricinus communis* he lists all the plant organs in which such crystal aggregates are claimed to be similarly situated. In summarizing he claims that calcium oxalate is never deposited in the plasma but only in the vacuole. As to the position and appearance of the nucleus he makes no special statement.

The material I have studied consists of spadices of various *Anthurium* species, fixed in Flemming's strong and medium chromic-osmic-acetic solutions for twenty-four and forty-eight hours. Sections were cut 5 μ, 7.5 μ, 12 μ, and 18 μ thick, and stained chiefly with the triple gentian-safranin-orange G stain, though the double fuchsin and iodine green stain was also used. Calcium oxalate crystals of the aggregate or stellate type were found in great abundance through the central axis of the spadix and in the perianth. These crystals give the ordinary test for calcium oxalate, i. e., solution in nitric acid and in hydrochloric acid without formation of gas bubbles. My drawings are all from preparations of *Anthurium grande*. Other species studied were *Anthurium acaule*, *A. Andreanum*, *A. gracile*, *A. Guildingii*, *A. magnificum*, *A. Olfersianum*, *A. scandens*, *A. Scherzerianum*, *A. variabile*, and a small unidentified epiphytic species from Panama growing in the Columbia University greenhouse. The

other species are growing in a plant house of the New York Botanical Gardens.

Cells with stellate crystals are not as prominent as raphide-bearing cells, which are also plentiful in this material. The latter are always greatly enlarged cells with prominent nuclei, as described by Miss Smith (**22**) for the orchids, while the former give little evidence of cell hypertrophy or abnormal nuclear size. In this connection it may be noted that Samuels (**19**), in a recent paper, reports finding in *Anthurium scandens* and *A. Scherzerianum* large raphide-containing cysts, which are pathological and arise as the result of the fusion of several cells and of their nuclei. Ordinary raphide-bearing cells also occur and differ from the cysts in that no nuclear or cell fusions occur.

In the older tissues of *Anthurium grande* the crystal aggregate fills almost the entire lumen of the cell and the nucleus can be seen near the wall between the points of the crystals, as described by Lloyd for *Ginkgo*. Smaller crystals are found in otherwise undifferentiated parenchymatic cells that are no larger than normal adjoining cells, as can be seen in FIG. 3. Their nuclei, though perhaps shifted to one side or perhaps more noticeably to one end of the cell, are of normal size, and give evidence from their appearance that they are still truly functional. They are usually spherical or ellipsoidal in shape. In sections stained with the triple stain the one or more nucleoli stand out sharply against the more dispersed chromatin as it appears in an ordinary resting nucleus (FIGS. 1, 2, 3).

The cells of these tissues are already vacuolated. Younger ones toward the tip of the spadix showed numerous vacuoles with the nucleus in the centre of the cell; the older cells have one large central vacuole with nucleus and primordial utricle lying next to the cell wall. All the pith cells of the central axis had reached the latter stage, while those in the perianth varied. Many were still in process of division, and small stellate crystals could be seen in cells adjoining those with spindle figures.

In FIG. 1 is shown a subepidermal cell from a perianth part with a comparatively small crystal group, little larger than the cell nucleus, whose nearly spherical shape and almost central position are quite evident. The cytoplasm shows numerous vacuoles and in one of these the crystal apparently lies, though the vacuolar membrane cannot be followed all the way round.

In FIG. 3 the crystal clearly lies in a normally spherical-appearing vacuole. As drawn, the tonoplast on the upper side overlaps the crystal, but that is the result of its being drawn at a higher plane. The primordial utricle next to the wall is quite distinct. By a slight shrinkage the plasma membrane has been sufficiently drawn away from the wall to become sharply distinguishable. The nucleus, which approximates the size of that in the normal cell next to it, lies imbedded in the cytoplasm, while the crystal appears as an inclusion in the vacuole. By the number of walls adjoining those of the cell (FIG. 1) it might appear that that cell was very much hypertrophied. However, it is merely so by contrast to the smaller epidermal cells by which it is bounded along two sides.

Cells containing larger crystal aggregates show a thin primordial utricle, as is usual in older cells, when a large vacuole occupies the centre of the cell. FIG. 4 shows two cells from the pith of the spadix. The one to the right is a normal parenchymatous cell, somewhat elongated, and lacking any stainable vacuolar content. The nucleus is appressed to the cell wall, lying in a primordial utricle that also contains scattered chloroplasts. The adjoining cell appears more isodiametric because of the large almost radially symmetric crystal aggregate, looking like a sunburst, that occupies its central region. There is little difference in the remaining contents of the two cells, cytoplasm, chloroplasts, and nuclei, are equally large and of normal appearance. Adjacent to the intercellular spaces the walls of the two cells are seen to be of the same thickness unlike those described by Lloyd in *Ginkgo*. He describes the large druse as surrounded by a thin cell wall which has never acquired the thickness of those of the living neighboring cells. It will be noticed that the intercellular spaces (FIG. 4) are smaller to the right of the normal cell than to the left of the crystal-containing cell due to the fact, however, that the former approaches a vascular bundle region where the cells are more closely crowded.

FIG. 5 represents a still larger crystal also from the pith region when the primordial utricle has become very scant, almost unnoticeable except as a plasma membrane, which however shows quite clearly in some places. The individual crystals extend almost to the cell wall into this thin layer and in some cases the colloidal mass extends inwards sheathing the crystal tips for a short distance.

As noted, Wakker considered the proof adequate that the origin of crystals is in the vacuole. Kohl (**8**), on the other hand, held to their origin in the mass of the colloidal cytoplasm itself. In classifying calcium oxalate crystals in respect to the positions they occupy in the plant cell he recognized three types. They may: (1) appear as inclusions in the protoplast; (2) be lodged in the membrane; or, finally, (3) be attached to the cell wall. If crystals may appear in the cell membrane and are surrounded by a cellulose sheath, Kohl considered it probable that they originate in the cell plasma, since only by its activity could the crystal be encapsuled by a cellulose sheath.

Pfeffer (**15**, p. 95) considered the possibility of a passage of crystals through the plasma. In the plasmodia of Myxomycetes he claims amoeboid movements serve mechanically in taking into the substance of the protoplasm foreign particles. These are carried to the interior and, penetrating the vacuoles, are expelled from time to time. Crystals like other solid bodies might be so transferred and in protoplasts bounded by a cell wall would collect in the cell sap.

The proof that crystals, either clearly visible in the vacuole or less evidently so, are surrounded by a plasma sheath is probably inadequate. The older observation of Payen (**14**) of aggregates of crystals so enclosed in the cells of Cacti needs confirmation. In general, acids have been used to first dissolve the salt and leave the crystal sheath. Such methods of determination involve the risk of inaccuracy, since the possibility that the so-called sheath is a precipitation or shrinkage product is not sufficiently considered. Osterhout (**12**) has shown that shrinkage may be caused by other means than the use of hypertonic solutions.

Deviations from the general occurrence of plasmolysis in a cell when placed in a solution whose osmotic pressure exceeded that of the cell sap led him to suspect that a contraction of the protoplasm might be due to the chemical action of a salt. This conception was confirmed by finding that plasmolysis of *Vaucheria* zoospores in a 0.0001 m. solution of NaCl was prevented when a little $CaCl_2$ was added. By putting in the minute amount of one molecule for every hundred molecules of NaCl the protoplasm of the algal cells showed no contraction even though the solutions reached one thousand times greater osmotic pressure

(0.1 m.). His interpretation is that the contraction was caused by the penetration of the NaCl producing chemical effects upon the protoplasm rather than by the greater osmotic pressure of the salt solution. This behavior Osterhout has called false plasmolysis. He (**13**) later described such effects from pure distilled water. There he explained the result as due to an increase in permeability of the plasma membrane, by which some or all of the substances which maintain the osmotic pressure of the cell diffuse out. An apparent "coagulation" of the protoplasm resulted which is not to be confused with true plasmolysis.

In this connection such a figure as FIG. 2 is interesting. The small crystal aggregate lies in a large central vacuole surrounded by the primordial utricle with nucleus, somewhat shrunken from the wall. A delicate strand running from one of the crystals to the vacuolar wall is noticeable, having stained yellow with orange. On other crystals also there appear very delicate similarly-staining extensions. If, as is generally conceded, (see Meyer, **10,** p. 57; Sharp, **21,** p. 135; Osborne, **11,** p. 7; and, especially for idioplasts, Heinricher, **4,** and Schneidler, **20**) and as is regarded as probable but not proven by Pfeffer (**15,** p. 82) there are soluble protein materials in the vacuole these would quite probably be coagulated by fixation and may account for such appearances. With our present inadequate knowledge of stains and tests for minute quantities of protein in the cell there is difficulty in deciding the true nature of such materials.

It is of interest here to note that the so-called Rosanoff crystals, although first found by Rosanoff (**16**) in the pith of *Kerria japonica* and *Ricinus communis*, were found but little later by him (**17**) in sacs accompanying the vascular bundles of the petioles of the Aroideae, among them *Anthurium rubricaule* and *A. Selloum*, as well as in the parts of the flower of *Encephalartos* and *Nelumbium*. His figures show stellate crystals of calcium oxalate connected with the cell wall by strands which he claimed are cellulose, "Cellulosebalken," or the crystal may simply project from the cell wall. By treating the cell with nitric acid which dissolved the oxalate of lime there remained the strands, and also what he considered to be the sheath that had surrounded the crystal. His figure of a cell so treated shows a shrunken mass and suggests that the protoplast may have suffered from the same traumatic effects as those described by Osterhout.

De la Rue (**2**) a little later gave further confirmation of Rosanoff's crystals. He reported them in the leaf of *Hoya carnosa* and in the petioles of *Pothos crassinervius* (*Anthurium Hookeri*) and *Philodendron pertusum*. In his rather crude figure (*f. 3*) of a cell of *Hoya carnosa* he includes a nucleus and chloroplasts. Rosanoff (**17**) gives a figure of a cell of *Anthurium Selloum* (*f. 4*) showing the nucleus lying somewhat beneath the crystal and in the conclusion of his paper states that he finds the nucleus unaltered in these crystal-bearing cells. Both of these statements were made in refuting the statement in an earlier text-book of Duchartre (**3**), "Les celles dans les quelles existent des cristaux ne refernment pas d'autres matières solides."

Wittlin (**24**) has also confirmed Rosanoff. In an extensive investigation of various tissues he frequently found the crystal with a cellulose sheath accompanied usually by cellulose strands. This was the case in the pith of stems of *Kerria japonica*, in the pith of internodes of *Caesalpinia Sapan*, and *Tilia* (tissue not mentioned). In the fundamental tissue of stems and petioles of *Philodendron pertusum* (*Monstera deliciosa*) and *P. "argyrea"*, and *Morus alba* (tissue also not mentioned), the strands were found to be very short and broad or lacking altogether. For his study he used fresh material and cut successive sections from the growing point backward. In younger regions of stems of *Kerria japonica*, about 1.5 mm. in thickness, he found the crystal lying in the plasma with the nucleus also visible. Cutting further he found successively larger crystals in cells whose plasma with the nucleus was contracted about the crystal, until in stems 2.5 mm. thick he found the crystals touching the cell wall. At this late stage in development the formation of the cellulose membrane about the crystal occurs, beginning at the point of contact of the crystal with the cell wall. With the growth of the cell a so-called foot is formed, which broadens and becomes stretched into a strand that pushes the crystal with its sheath towards the center of the cell. The plasma is partly used and partly displaced. The nucleus becomes invisible at the first appearance of the cellulose strands (**24**, *pl. 1, f. 1–4*). In *Caesalpinia Sapan* similar appearances were found although the elaioplasts and plasma persist after the nucleus becomes invisible. The presence of the nucleus in cells containing small crystals and its later disappearance he regards as constant.

Johow (**7**) studied members of the families Aroidaceae, Commelinaceae, Amaryllidaceae, Iridaceae, and Orchidaceae, with the object of determining whether nuclei or any protoplasmic body were present in mature tissue cells. He worked with fresh material, using staining reagents to differentiate the cell content. In such cases as the raphide cells, where it was impossible to investigate sections of living tissue because the rows of sacs could not be kept intact for their whole length, he had recourse to alcoholic material, of which single cells were isolated by maceration methods and then stained. Johow reached the conclusion that in all secretory reservoirs observed by him, including slime-containing raphide sacs, *drusen* cells, latex-containing sacs, tannin sacs and tannin-containing septate latex tubes, protoplasm and nucleus were regularly present. Of the aroids he observed *Anthurium sagittatum* and *Philodendron cordifolium* and found in older stems and leaf petioles the characteristic Rosanoff crystals. He describes them as filling almost entirely the lumen of the cell, being connected by cellulose strands to the wall and enclosed by a cellulose membrane. As Rosanoff had observed, he too found the unchanged nucleus with a nucleolus. He points out that the nucleus lies in a well developed primordial utricle along the cell wall and not adjacent to the crystal.

Kohl (**8**), also working in the petiole of *Anthurium Scherzerianum*, found nuclei lying in the cytoplasm of the crystal cells and confirmed Rosanoff's findings as to the presence of a cellulose sheath about the crystals (see also Meyer, **10,** p. 381) but the same method of treatment by nitric acid was employed. I have sections of an *Anthurium* petiole which give data bearing on the problem of the cellulose sheath on which I shall report in a later paper.

Kohl is very clear on the question here involved as to the presence of the nucleus in the primordial utricle and outside the crystal group. Johow's criticism of the text-books of Sachs (**18**) and De Bary (**1**) for assuming that there are no other solid bodies in a crystal-containing cell is entirely justified.

As for the nucleus in *Anthurium grande*, it persists intact in the cell after the crystal has become a conspicuous stellate structure in a vacuole. When the size of the crystal is such as to occupy almost the entire lumen of the cell the nucleus is

still in evidence in a thin primordial utricle not only in this species but in the others mentioned earlier. In these forms there is certainly no evidence that the nucleus ever forms the centre about which a stellate group of crystals develops.

In conclusion I wish to thank Professor R. A. Harper for his suggestions and careful criticism of this work.

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Explanation of plate 20

The figures were drawn with the aid of a camera lucida from sections 12 μ and 18 μ thick of the spadix of *Anthurium grande*. In representing the crystals no attempt was made to show the crystals in perspective. Apices merely are outlined. FIGS. 1, 2 and 3 are magnified approximately 1950 times; FIGS. 4 and 5, approximately 980 times.

FIG. 1. Subepidermal cell from a perianth part with nucleus almost centrally placed in the vacuolated cytoplasm. A small stellate crystal appears to lie in one of these vacuoles.

FIG. 2. Crystal-containing cell from the perianth. The protoplast is shrunken and drawn away from the cell wall but in the large central vacuole appears a small crystal with a very delicate strand-like attachment to the vacuolar membrane.

FIG. 3. A normal parenchymatous cell from a perianth part with a crystal-containing cell of approximately equal size adjoining it.

FIG. 4. Two cells from the pith of the central axis of the spadix, contrasting the isodiametric shape of the larger aggregate crystal-containing cell with the adjoining cell. Nuclei and primordial utricle with chloroplasts are comparable in the two.

FIG. 5. A large aggregate of crystals occupying almost the entire lumen of the cell. Some of the crystals nearly reach the cell wall by extending into the thin primordial utricle. Nucleus still clearly visible.

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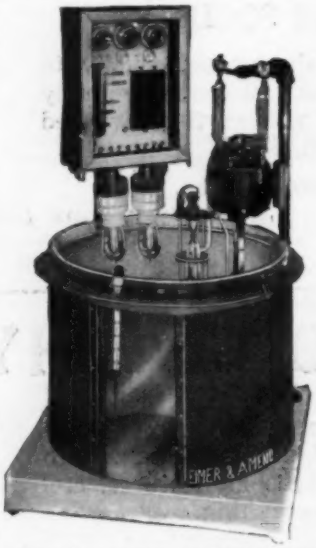

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